

DIET, FEEDING HABITS, AND DIEL FEEDING CHRONOLOGY OF THE BONNETHEAD SHARK, *SPHYRNA TIBURO*, IN SOUTHWEST FLORIDA

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ABSTRACT

The diet, feeding habits, and diel feeding chronology of the bonnethead shark, *Sphyrna tiburo*, in Tampa Bay and Charlotte Harbor, two estuaries of southwest Florida, were investigated through analysis of stomach contents. The diet was very homogeneous and was dominated by crustaceans, consisting mostly of blue crabs, *Callinectes sapidus*, followed by seagrasses and traces of mollusks, teleosts, and other material. A significant prey/predator length relationship was found for *C. sapidus* and *S. tiburo*. Contingency table analysis and measures of dietary overlap and diet breadth were used to detect seasonal, sex, size, locality, and habitat-related quantitative differences in stomach contents. Results suggest that *S. tiburo* is a specialist that undergoes dietary shifts depending on season and habitat. Discontinuity of feeding was investigated using two different statistical techniques and results varied by method, revealing the shortcomings of the most commonly used approach and the limited value of considering only stomach contents weight to investigate diel feeding chronology.

The bonnethead shark, *Sphyrna tiburo*, is an abundant small coastal shark of the hammerhead family (Sphyrnidae). It has been reported in the western Atlantic from southern Brazil to North Carolina (Bigelow and Schroeder, 1948) and is commonly found in the shallow estuaries of Florida's Gulf of Mexico coast, especially during the warmer months (Parsons, 1987), although Springer (1938), Bigelow and Schroeder (1948) and Clark and von Schmidt (1965) found midsummer catches of *S. tiburo* along the Gulf coast of Florida to be scarce, probably due to gear type and habitat fished.

Few quantitative data on the diet of *S. tiburo* have been published. Gunter (1945) reported six specimens taken from Aransas Pass, Texas, to contain an average of 2.5 blue crabs, *Callinectes sapidus*, in their stomachs. Bigelow and Schroeder (1948) reported *S. tiburo* of the western north Atlantic to feed on crabs plus shrimps, isopods, barnacles, mollusks, cephalopods, small fish and seaweeds, but no quantitative data were given. Clark and von Schmidt (1965) reported *C. sapidus* in the stomachs of several specimens from the central Gulf coast of Florida. Unpublished data of Parsons (1987) showed cephalopods to be the most common prey of *S. tiburo* in Florida Bay, occurring in 34% of 53 stomachs, and *C. sapidus* the most common in Tampa Bay, occurring in 91% of 99 stomachs. Additionally, he found seagrasses in 47% and 85% of the same groups of sharks, respectively.

The purpose of our study was to quantify seasonal, size, sex, and habitat-related dietary shifts, and diel feeding chronology and other feeding habits of *S. tiburo* in Tampa Bay and Charlotte Harbor, two large estuaries of southwest Florida. Using *S. tiburo* as a model, we also sought to advance quantitative methods applied in feeding studies of elasmobranch fishes.

MATERIALS AND METHODS

Specimen Collection and Analysis.—All sharks were caught between May 1992 and November 1993 using gill nets set in Tampa Bay, Charlotte Harbor, or adjacent coastal waters of the Gulf of Mexico (Fig. 1). Use of gill nets avoids the bias of attraction by bait, which yields greater percentages of sharks with empty stomachs (Gruber, 1984; Cortés and Gruber, 1990). Nets were set for 0.8–1.5 h in depths ranging from 0.3–7.0 m and then retrieved. Sharks were caught day and night, and stomach

samples were taken at times ranging over the full 24-h diel cycle. All live sharks were sexed, measured (precaudal, fork, total, and stretch total lengths to the nearest cm), weighed (to the nearest 0.1 kg), tagged and released. Dead sharks were measured, weighed, and examined internally, and tissues of interest, including the entire stomach with its contents, were removed. Stage of maturity was determined by examination of external and internal reproductive organs. Stomachs were stored by freezing until the contents could be examined in the laboratory. Stomachs of a few live *S. tiburo* were everted following the technique of Cortés and Gruber (1990). In all, stomach contents from 355 *S. tiburo* specimens (130 males and 225 females) were collected. Males ranged from 33 to 71 cm precaudal length (PCL)¹ and from 0.4 to 4.0 kg body weight. Females ranged from 31 to 84 cm PCL and from 0.4 to 9.0 kg body weight.

In the laboratory, samples were thawed and stomach contents were separated, counted, weighed (to the nearest 0.01 g), and measured (to the nearest mm) when possible, and then preserved in 70% isopropanol. Prey items were identified to the lowest taxon possible. Identifiable plant material was sorted by species and each plant species was weighed collectively and counted as a single item. Length and width of crab carapaces were measured to the nearest mm; although carapace width is more commonly used, we measured carapace length whenever the lateral extensions of the carapace were fragmented. To estimate carapace width in those cases, a length/width regression was calculated using intact specimens of *C. sapidus* from the shark stomachs.

Data Analysis.—Diet composition was analyzed using a variety of indices (Pinkas et al., 1971; Hyslop, 1980) comprising the numerical index (%N), the gravimetric index based on wet weight (%W), the frequency of occurrence (%O), and the index of relative importance (IRI), which incorporates the three previous indices and was expressed as a percentage (%IRI).

Contingency table analysis (Crow, 1981) was used to test for seasonality and size-related variations in the diet of *S. tiburo*. To avoid small expected frequencies for χ^2 tests, numbers of prey items were pooled into six categories: blue crabs, other crabs, shrimps, miscellaneous prey items (mollusks, teleosts, and all other food items not included in the other categories), plants, and unidentifiable digested food. χ^2 values then were calculated for each row and column, and a significant grand total χ^2 statistic indicated a significant difference in the proportions of prey species in the diets of the sharks among seasons or size classes. The most significantly different groups, i.e., the groups with the largest row or column sum of χ^2 , were identified and eliminated from further analysis. A posteriori tests were rerun until all sources of variability were identified.

Dietary overlap was calculated using the Spearman rank correlation coefficient (r_s) as described by Fritz (1974) and Horn's (1966) index of overlap (R_o ; Krebs, 1989). Based upon the observed range of food types, prey items were pooled for analysis into seven categories (blue crabs, other crabs, shrimps, squids, teleosts, plants, and unidentifiable digested food) and the contribution of each prey category to the diet expressed as %IRI. For r_s , the null hypothesis was that the diets of the two compared groups are different ($r_s = 0$); therefore, if r_s was significant, the null hypothesis was rejected, indicating that the diets are similar. In the case of R_o , values vary between 0 (no categories in common) and 1 (identical proportional composition).

Diet breadth was calculated using Levin's standardized index (B_s ; Krebs, 1989), the Shannon-Wiener measure with evenness (J' ; Krebs, 1989) and a combined index (CI) that we derived as the average of the two. Prey types were pooled into the same categories as above and %IRI was used in the calculations. All three indices are standardized on a scale from 0 to 1, with larger values indicating larger diet breadth.

Stomach content weight was expressed as a percentage of shark wet body weight (%BW). The distribution of these relative weights consistently failed normality and homoscedasticity tests (Sokal and Rohlf, 1981), and so non-parametric Mann-Whitney *U*-tests were used to detect differences in median %BW between sexes, immature vs. mature stages, seasons, sizes (in arbitrary 15 cm increments of < 45 cm PCL, 45–59 cm PCL, 60–74 cm PCL, and > 74 cm PCL), habitats (inside the bays vs. off the beaches), and locations (Tampa Bay vs. Charlotte Harbor).

To test for discontinuity in feeding over time of day, two different approaches were used. First, the times at which stomach contents were sampled were grouped into eight successive 3-h intervals of the 24-h diel cycle, and stomach content weights (as %BW) corresponding to each sampling time then were subjected to a Kruskal-Wallis test. If a significant difference was found, a posteriori comparisons were performed for each pair of consecutive median values using Mann-Whitney *U*-tests. To assess the influence that duration and choice of the time interval may have on testing for feeding continuity, sampling times were redistributed into two additional sets of eight successive 3-h intervals and four sets of six successive 4-h intervals, and the stomach contents data again were subjected to

¹ To convert from PCL to other length measurements in *S. tiburo*, simple linear regressions were performed between PCL and fork length (FL), total length (TL), and stretch total length (STL). Stretch total length is the distance from tip of snout to tip of tail with tail pulled back along the rostro-caudal axis. Formulae are as follows: FL = 1.066PCL + 1.077 (n = 705, r = 0.998); TL = 1.166PCL + 6.553 (n = 705, r = 0.992); STL = 1.245PCL + 6.710 (n = 705, r = 0.997).

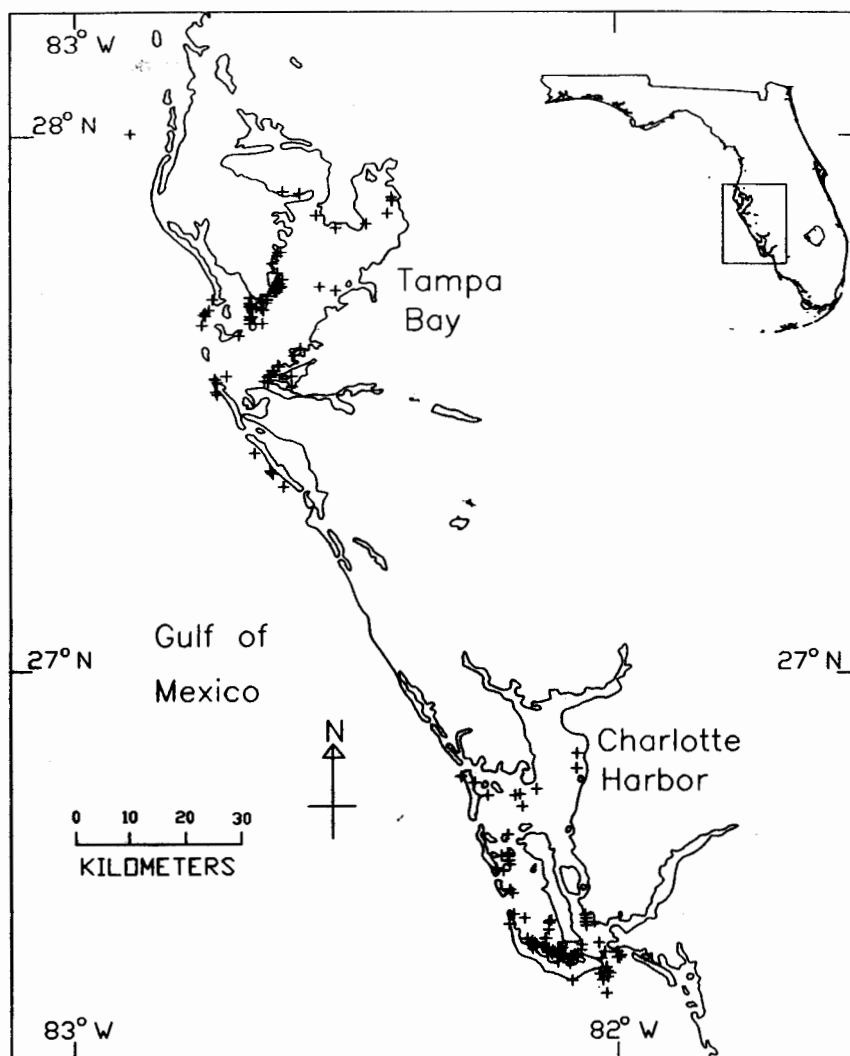


Figure 1. Map of areas fished on the southwest gulf coast of Florida. Each cross (+) indicates a collection site for bonnethead sharks, *Sphyrna tiburo*.

Kruskal-Wallis and Mann-Whitney *U*-tests. In the second approach, one-way analysis of covariance (ANCOVA) was used to test for discontinuity in feeding activity, as described by Jenkins and Green (1977). This method relates stomach content weight to fish weight and compares the resulting regressions for each time interval under consideration. The test for difference in intercepts given common slopes is the test for among-time differences in stomach contents adjusted for fish size. To normalize our data, the transformation $\ln + 1$ (ln, natural logarithm) was applied to stomach content weights and shark weights. One-way ANCOVA's were run for each of the three sets of eight 3-h intervals and the four sets of six 4-h intervals.

RESULTS

Diet Composition.—Of the 355 shark stomachs examined, 338 contained items and 17 (5%) were empty. Crustaceans were the dominant food category on a

Table 1. Diet composition of the bonnethead shark, *Sphyrna tiburo*, in southwest Florida expressed as percent by number (%N), percent weight (%W), frequency of occurrence (%O), and the index of relative importance on a percent basis (%IRI)

Prey items	%N	%W	%O	%IRI*
Crustacea	63.36	82.86	88.92	84.86
Portunidae				
<i>Callinectes sapidus</i>	54.22	71.10	71.43	85.70
<i>Arenaeus cribrarius</i>	0.20	0.34	0.58	T
Paguridae spp.	0.10	0.01	0.29	T
Majidae				
<i>Libinia dubia</i>	0.10	0.22	0.29	T
Xanthidae				
<i>Menippe mercenaria</i>	0.79	0.56	2.33	0.03
Leucosiidae				
<i>Persephona punctata</i>	0.20	0.04	0.29	T
Unidentified crabs	4.77	7.40	13.99	1.63
Squillidae				
<i>Squilla empusa</i>	2.18	2.97	5.83	0.29
Penaeidae				
<i>Penaeus duorarum</i>	0.40	0.09	1.17	0.01
Unidentified shrimp	0.40	0.13	1.17	0.01
Mollusca	0.80	0.83	2.33	T
Cephalopoda	0.40	0.82	1.17	T
Loliginidae				
<i>Loligo pealei</i>	0.20	0.70	0.58	0.01
Unidentified squid	0.20	0.12	0.58	T
Unidentified gastropod	0.40	0.01	1.17	0.01
Osteichthyes	0.50	0.70	1.46	T
Ophichthidae	0.20	0.09	0.58	T
Unidentified teleost	0.30	0.61	0.87	0.01
Angiospermae	26.70	7.03	55.98	12.36
<i>Thalassia testudinum</i>	5.16	0.67	15.16	0.85
<i>Syringodium filiforme</i>	10.72	3.80	31.49	4.38
<i>Halodule wrightii</i>	10.82	2.56	31.78	4.07
Miscellaneous	8.64	8.56	24.78	2.78
Unidentifiable digested food	7.05	7.98	20.70	2.98
Non-food material	0.79	0.41	2.33	0.03
Other plant material	0.70	0.02	2.04	1.47
Merostomata				
<i>Limulus polyphemus</i>	0.10	0.15	0.29	T

* The right column is the %IRI for the higher prey category levels considered (Crustacea, Mollusca, Osteichthyes, Angiospermae, and Miscellaneous).

T = trace amounts (<0.01 %IRI).

numerical (63.4%), wet weight (82.9%) and occurrence basis (88.9%; Table 1 and Fig. 2) and included at least nine different species representing seven families. Angiosperms consisted of three species (*Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*) occurring in 56% of the stomachs and was the second most important category numerically (26.7%) and the third by weight (7%). The %IRI showed that crustaceans make up 85% of the diet, followed by angiosperms (12.4%), miscellaneous material (mostly unidentifiable digested food; 2.8%) and traces of mollusks (squids) and teleosts (including snake eels [Ophichthidae]). Among crustaceans the main item was *C. sapidus* (85.7% in %IRI). The mantis shrimp, *Squilla empusa*, occurred in about 6% of the stomachs, and the pink shrimp, *Penaeus duorarum*, and other species of crabs represented a very small portion of the diet of *S. tiburo* (Table 1).

Seasonal variations in the %IRI of prey species and categories indicated that crustaceans were the dominant food category and *C. sapidus* the dominant prey

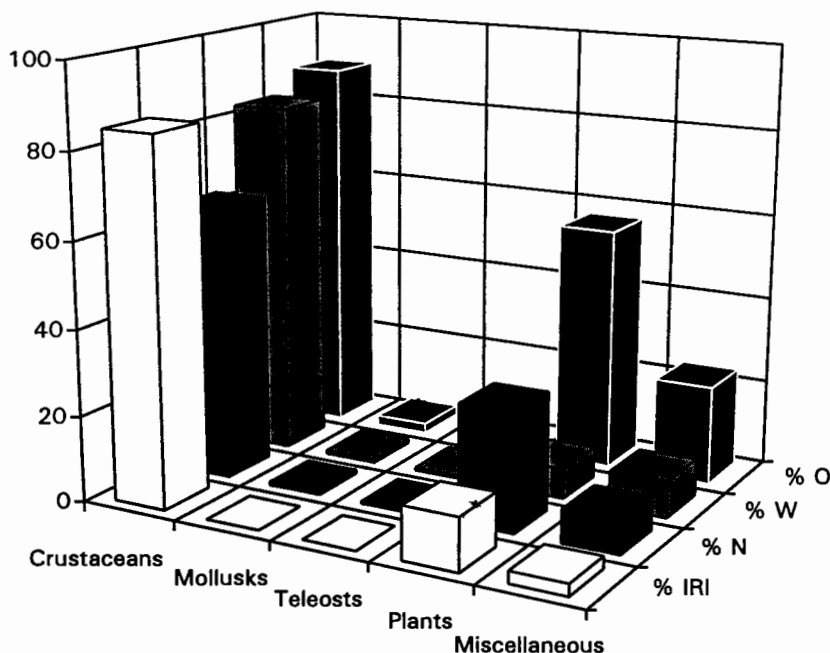


Figure 2. Main food categories of *Sphyrna tiburo* in southwest Florida expressed as percent by number (%N), percent by weight (%W), frequency of occurrence (%O), and the index of relative importance on a percent basis (%IRI). "Miscellaneous" consists of mostly unidentifiable digested food.

species in all seasons (Table 2). In winter, however, crustaceans and *C. sapidus* comprised only about 46% and 43% of the diet, respectively, while there was a relatively large proportion of unidentifiable digested food (35%), probably due to slow gastric evacuation at low winter temperatures. In fall, prey species diversity increased, with two species of crabs (the spider crab, *Libinia dubia*, and the purse crab, *Persephona punctata*) and at least one cephalopod species (the squid *Loligo pealei*) appearing in the diet, although in small proportions. In addition, the stone crab, *Menippe mercenaria*, was found in a larger proportion in fall than in spring and summer.

Crustaceans and *C. sapidus* also were the dominant prey category and species in all shark size classes (Table 3). For sharks < 45 cm PCL, crustaceans and *C. sapidus* amounted to only 67.9% and 65%, respectively, of the diet, with unidentifiable digested food totalling 16.9%. The speckled swim crab, *Arenaeus cribrarius*, appeared only in the < 45 cm PCL class and stone crabs also were more important in this size category. No teleosts appeared in sharks < 45 cm PCL. Remains of a horseshoe crab, *Limulus polyphemus* (Merostomata), were found in the stomach of one 74 cm PCL specimen of *S. tiburo*.

Contingency table analysis revealed significant differences in the proportions of food categories among seasons ($\chi^2 = 83.2$, 15 df, $P < 0.001$; Table 4). The main source of variation among food types came from unidentifiable digested food, and among seasons from winter and to a lesser extent fall. Subsequent analyses revealed that the main sources of variability came from unidentifiable digested food (which was overrepresented in winter), miscellaneous prey (overrepresented in fall), and plants (underrepresented in spring and overrepresented

Table 2. Seasonal variation in the index of relative importance on a percent basis (%IRI) of prey items in the diet of *Sphyrna tiburo* in southwest Florida

Prey items	Winter (14)*	Spring (181)*	Summer (123)*	Fall (25)*
Crustacea	45.95	90.96	82.40	89.74
Portunidae				
<i>Callinectes sapidus</i>	43.17	89.28	80.22	86.62
<i>Arenaeus cribrarius</i>	—	—	0.02	—
Paguridae spp.	—	T	—	—
Majidae				
<i>Libinia dubia</i>	—	—	—	0.23
Xanthidae				
<i>Menippe mercenaria</i>	—	0.01	0.09	0.18
Leucosiidae				
<i>Persephona punctata</i>	—	—	—	0.17
Unidentified crabs	2.78	1.21	1.94	2.12
Squillidae				
<i>Squilla empusa</i>	—	0.43	0.12	0.42
Penaeidae				
<i>Penaeus duorarum</i>	—	0.01	0.01	—
Unidentified shrimp	—	0.01	T	—
Mollusca	—	0.01	T	1.78
Cephalopoda	—	—	—	1.78
Loliginidae				
<i>Loligo pealei</i>	—	—	—	1.32
Unidentified squid	—	—	—	0.46
Unidentified gastropod	—	0.01	T	—
Osteichthyes	—	0.01	0.03	—
Ophichthidae	—	0.01	—	—
Unidentified teleost	—	T	0.03	—
Angiospermae	18.61	7.06	14.72	4.75
<i>Thalassia testudinum</i>	0.15	0.38	2.45	0.09
<i>Syringodium filiforme</i>	0.14	3.04	8.49	2.13
<i>Halodule wrightii</i>	18.32	3.64	3.78	2.53
Miscellaneous	35.44	1.98	2.83	3.74
Unidentifiable digested food	35.44	1.94	2.79	3.49
Non-food material	—	0.02	0.04	0.07
Other plant material	—	0.02	T	—
Merostomata				
<i>Limulus polyphemus</i>	—	—	—	0.18

* Number of stomachs containing food.
T = trace amounts (<0.01 %IRI).

in summer). When winter, fall, and plants were eliminated, no significant differences were found ($\chi^2 = 5.0$, 4 df, $P > 0.05$).

Significant differences also were found in the proportions of food types consumed by sharks of different sizes ($\chi^2 = 32.5$, 15 df, $P < 0.01$; Table 5). The main source of variability came from the smallest sharks (< 45 cm PCL) which had more unidentifiable digested food than expected. When the < 45 cm PCL size class was eliminated, results were not significant ($\chi^2 = 15.5$, 10 df, $P > 0.05$).

Diet Overlap and Diet Breadth.—The Spearman rank correlation coefficient (r_s) and Horn's index of overlap (R_o) indicated a high degree of overlap in the diet between locations (Tampa Bay vs. Charlotte Harbor), seasons, and shark size and sex (Table 6). Only the habitat comparison yielded a non-significant value of r_s and the lowest value of R_o (0.181), indicating that the diet of *S. tiburo* caught inside the bays was quantitatively different from that of *S. tiburo* caught off the beaches in the open Gulf. This habitat-related dietary difference included a higher

Table 3. Variation in the index of relative importance on a percent basis (%IRI) of prey items in the diet of four length classes of *Sphyrna tiburo* in southwest Florida

Prey items	Shark precaudal length (cm)			
	<45 (33)*	45-59 (208)*	60-74 (91)*	>74 (11)*
Crustacea	67.88	88.64	85.80	89.67
Portunidae				
<i>Callinectes sapidus</i>	64.99	86.05	84.28	89.35
<i>Arenaeus cribrarius</i>	1.06	—	—	—
Paguridae spp.	—	T	—	—
Majidae				
<i>Libinia dubia</i>	—	—	0.01	—
Xanthidae				
<i>Menippe mercenaria</i>	0.33	0.01	0.09	—
Leucosiidae				
<i>Persephona punctata</i>	—	T	—	—
Unidentified crabs	0.98	2.15	1.20	0.32
Squillidae				
<i>Squilla empusa</i>	0.38	0.41	0.22	—
Penaeidae				
<i>Penaeus duorarum</i>	0.07	0.01	—	—
Unidentified shrimp	0.07	0.01	—	—
Mollusca	—	0.03	0.02	—
Cephalopoda	—	0.03	—	—
Loliginidae				
<i>Loligo pealei</i>	—	0.02	—	—
Unidentified squid	—	0.01	—	—
Unidentified gastropod	—	T	0.02	—
Osteichthyes	—	T	0.06	—
Ophichthidae	—	—	0.02	—
Unidentified teleost	—	T	0.04	—
Angiospermae	15.19	7.83	13.29	9.34
<i>Thalassia testudinum</i>	1.50	0.60	1.32	1.70
<i>Syringodium filiforme</i>	3.02	3.45	7.22	3.52
<i>Halodule wrightii</i>	10.67	3.78	4.75	4.12
Miscellaneous	16.94	3.50	1.92	0.98
Unidentifiable digested food	16.88	3.43	1.88	0.98
Non-food material	—	0.04	0.04	—
Other plant material	0.06	0.03	—	—
Merostomata				
<i>Limulus polyphemus</i>	—	—	0.01	—

* Number of stomachs containing food.
T = trace amounts (<0.01 %IRI).

Table 4. Contingency table analysis of the seasonal variation of six different categories of food items found in the stomachs of *Sphyrna tiburo* from southwest Florida. Values shown are observed numbers. The χ^2 statistic is highly significant (***) $P < 0.001$.

Prey type	Winter	Spring	Summer	Fall	N _i	χ^2
Blue crabs	10	320	168	42	540	11.87
Other crabs	3	28	23	8	62	3.75
Shrimps	0	19	8	2	29	2.39
Miscellaneous*	0	6	3	5	14	17.22
Plants	13	128	124	11	276	14.37
Unid. digested food	12	30	25	4	71	33.60
N _j	38	531	351	72	992	
χ^2	39.55	9.52	11.22	22.93		83.2***

* Includes mollusks, teleosts, and all other food items not found in the other categories.

Table 5. Contingency table analysis of the variations of six different categories of food items found in the stomachs of four size-classes (precaudal length) of *Sphyrna tiburo* from southwest Florida. Values shown are observed numbers. The χ^2 statistic is highly significant (** $P < 0.01$).

Prey type	<45 cm	45–59 cm	60–74 cm	>74 cm	N _i	χ^2
Blue crabs	28	368	123	21	540	7.34
Other crabs	7	39	15	1	62	1.82
Shrimps	3	21	5	0	29	2.42
Miscellaneous*	0	7	7	0	14	5.33
Plants	25	155	85	11	276	6.68
Unid. digested food	12	41	16	2	71	8.89
N _j	75	631	251	35	992	
χ^2	15.54	5.31	9.98	2.63		32.5**

* Includes mollusks, teleosts, and all other food items not found in the other categories.

proportion of shrimps and crabs other than *C. sapidus* in the stomachs of sharks caught off the beaches vs. those caught inside the bays. Among seasons, the lowest r_s values (0.892, $P < 0.05$) were obtained in the spring/fall and summer/fall comparisons, while the lowest R_o values were obtained in the winter/spring, winter/summer, and winter/fall comparisons, indicating that most of the variation in the diet occurred during fall and winter. Diet overlap was very high among all shark size classes.

The largest values of diet breadth (B_s , J' , and CI) were those corresponding to winter, beach, and the < 45 cm PCL shark size class, respectively (Table 7). These higher values are probably due to small sample sizes in the cases of winter ($N = 13$) and beach ($N = 16$), and the large amount of unidentifiable digested food and smaller proportion of *C. sapidus* in the diet of *S. tiburo* from winter, beach, and < 45 cm PCL.

Prey/Predator Length Relationship.—The best description of blue crab carapace length vs. shark PCL was obtained with a second order polynomial equation (Fig. 3). Variability in carapace length increased with increasing shark length. The

Table 6. Values of diet overlap obtained with the Spearman rank correlation coefficient (r_s) and Horn's index of overlap (R_o), calculated from the %IRI (index of relative importance expressed as a percent) of seven pooled food categories in stomach contents of *Sphyrna tiburo* from southwest Florida. Sexes, locations (Tampa Bay vs. Charlotte Harbor), habitats (beach vs. bay), seasons, and four size classes (precaudal lengths) are compared. Sample sizes are given in parentheses. Significant r_s values: ** $P < 0.01$; * $P < 0.05$.

Groups compared	r_s	R_o
Males (130) / Females (225)	0.928*	0.978
Tampa Bay (220) / Charlotte Harbor (131)	0.964**	0.970
Beach (16) / Bay (339)	0.660	0.181
Winter (13) / Spring (194)	0.957**	0.782
Winter (13) / Summer (123)	0.957**	0.838
Winter (13) / Fall (25)	0.957**	0.849
Spring (194) / Summer (123)	1.000**	0.983
Spring (194) / Fall (25)	0.892*	0.984
Summer (123) / Fall (25)	0.892*	0.969
<45 cm (40) / 45–59 cm (214)	0.974**	0.946
<45 cm (40) / 60–74 cm (90)	0.974**	0.939
<45 cm (40) / >74 cm (11)	0.962**	0.910
45–59 cm (214) / 60–74 cm (90)	0.964**	0.994
45–59 cm (214) / >74 cm (11)	0.979**	0.986
60–74 cm (90) / >74 cm (11)	0.979**	0.993

Table 7. Values of diet breadth obtained with Levin's standardized index (B_s), the Shannon-Wiener measure with evenness (J'), and a combined index ($CI = (B_s + J')/2$), calculated from the %IRI (index of relative importance expressed as a percent) of seven pooled food categories in stomach contents of *Sphyrna tiburo* from Southwest Florida. Values for sexes, locations (Tampa Bay vs. Charlotte Harbor), habitats (beach vs. bay), seasons, and four size classes (precaudal lengths) are presented. Sample sizes are given in parentheses.

Item	B_s	J'	CI
Males (130)	0.04	0.24	0.14
Females (225)	0.07	0.31	0.19
Tampa Bay (220)	0.04	0.22	0.13
Charlotte Harbor (131)	0.11	0.38	0.24
Beach (16)	0.22	0.52	0.37
Bay (339)	0.05	0.27	0.16
Winter (13)	0.31	0.59	0.45
Spring (194)	0.04	0.22	0.13
Summer (123)	0.08	0.33	0.21
Fall (25)	0.05	0.30	0.18
<45 cm (40)	0.18	0.50	0.34
45–59 cm (214)	0.06	0.28	0.17
60–74 cm (40)	0.06	0.28	0.17
>74 cm (11)	0.04	0.20	0.12

relationship between carapace length and width in *C. sapidus* was best described by the linear equation $L_c = 3.025 + 0.467W_c$ ($N = 139$, $r = 0.98$), where L_c is carapace length and W_c is carapace width. Carapace length of *C. sapidus* in the stomachs of *S. tiburo* ranged from 9 to 60 mm with most measuring between 14

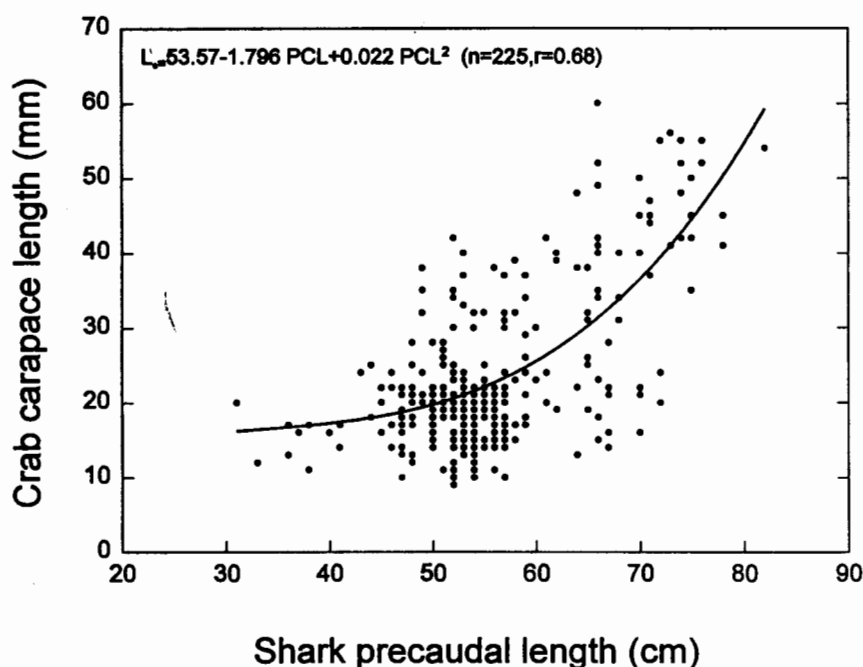


Figure 3. Prey/predator length relationship for blue crabs, *Callinectes sapidus*, and *Sphyrna tiburo* from southwest Florida. L_c is crab carapace length; PCL is shark precaudal length.

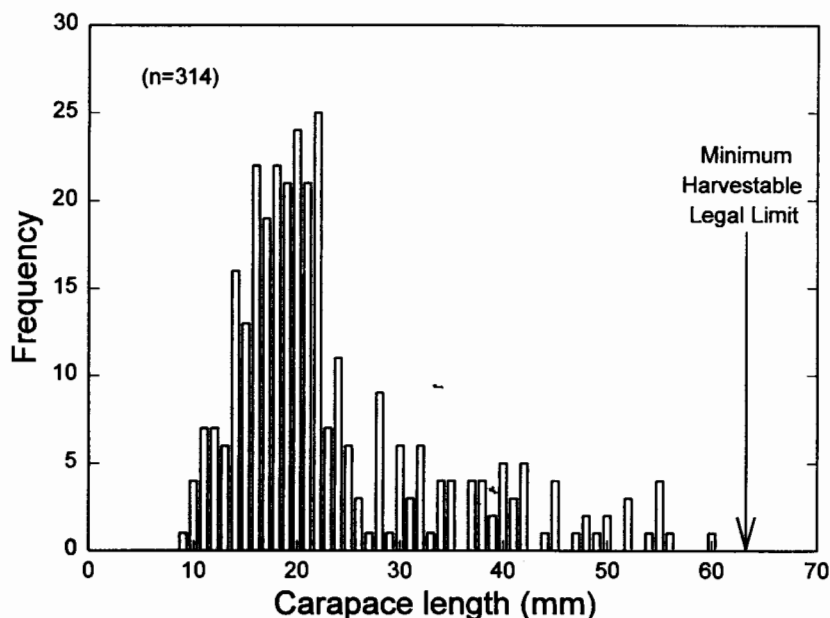


Figure 4. Length-frequency distribution of *Callinectes sapidus* carapaces from stomachs of *Sphyrna tiburo* collected in southwest Florida. The arrow indicates the minimum legally harvestable size of blue crab in the state of Florida.

and 24 mm (Fig. 4). All *C. sapidus* prey items were smaller than the legally harvestable minimum size of 62.3 mm carapace length (converted from legal minimum width of 5 in or 127 mm) for *C. sapidus* in the state of Florida (Fig. 4), indicating that bonnethead sharks and commercial fishermen do not compete directly for the same size classes of blue crabs in southwest Florida.

Food Consumption and Diel Feeding Chronology.—Stomach content weight (as %BW) of females was higher than that of males ($P < 0.001$; Table 8). Subsequent analyses revealed that immature males (usually < 50 – 55 cm PCL) had significantly less food in their stomachs than mature males ($P = 0.018$) and were the cause of this difference (Table 8). No significant differences in stomach content weight were found between sharks caught in Tampa Bay and Charlotte Harbor ($P = 0.504$), or between sharks caught inside the bays and off the beaches ($P = 0.390$). Among seasons, stomach content weight was significantly higher in winter than in spring ($P = 0.009$) or summer ($P = 0.007$), probably affected by the small sample size ($N = 13$) but possibly also due to slower gastric evacuation of *S. tiburo* in winter. The largest size-related differences were between the < 45 cm PCL and the 60–74 cm PCL classes ($P = 0.004$). The median amount of food consumed increased with increasing shark size, ranging from 1.03 %BW for sharks < 45 cm PCL to 2.56 %BW for sharks > 74 cm PCL.

Kruskal-Wallis tests revealed that the median amount of food in the stomach was significantly different ($P < 0.05$) over two of the three sets of eight 3-h intervals, and over three of the four sets of six 4-h intervals (Fig. 5). For the 3-h intervals, significant decreases (Mann-Whitney U -test, $P < 0.05$) in stomach content weights were observed in early morning (04:30–07:30 and 06:30–09:30), followed by an increasing trend extending until 16:30, 17:30, and 18:30, depend-

Table 8. Results of Mann-Whitney *U*-tests comparing stomach content weights (expressed as %BW) of *Sphyrna tiburo* from southwest Florida. Sexes, locations (Tampa Bay vs. Charlotte Harbor), habitats (beach vs. bay), seasons, and four size classes (precaudal lengths) are compared. Sample sizes are given in parentheses. Significant *P* values of the Mann-Whitney statistic (*U*_i) are denoted by: * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001.

Groups compared		<i>U</i> _i	<i>P</i> value
Tampa Bay (220)	/ Charlotte Harbor (131)	22,821	0.504
Beach (16)	/ Bay (339)	1,549	0.390
Winter (13)	/ Spring (194)	1,768	0.009**
Winter (13)	/ Summer (123)	1,106	0.007**
Winter (13)	/ Fall (25)	253	0.205
Spring (194)	/ Summer (123)	18,102	0.934
Spring (194)	/ Fall (25)	2,951	0.119
Summer (123)	/ Fall (25)	1,835	0.203
<45 cm (40)	/ 45–59 cm (214)	3,540	0.081
<45 cm (40)	/ 60–74 cm (90)	1,570	0.004**
<45 cm (40)	/ >74 cm (11)	274	0.024*
45–59 cm (214)	/ 60–74 cm (90)	14,834	0.011*
45–59 cm (214)	/ >74 cm (11)	1,396	0.038*
60–74 cm (90)	/ >74 cm (11)	539	0.200
Immature females (157)	/ Mature females (68)	7,977	0.514
Immature females (157)	/ Immature males (65)	5,654	<0.001***
Mature females (68)	/ Immature males (65)	3,515	<0.001***
Immature females (157)	/ Mature males (65)	6,625	0.153
Mature females (68)	/ Mature males (65)	3,939	0.061
Immature males (65)	/ Mature males (65)	3,747	0.018*
Immature females (157)	/ All males (130)	16,099	0.004**
Mature females (68)	/ All males (130)	7,821	0.002**
All males (130)	/ All females (225)	18,402	<0.001***

ing on the set of eight 3-h intervals considered (Fig. 5). Another significant decrease (Mann-Whitney *U*-test, *P* < 0.05) in stomach content weight was then observed in the evening (18:30–21:30), although at 21:30 sample size was small (*N* = 7). For the 4-h intervals, significant decreases (Mann-Whitney *U*-test, *P* < 0.05) in stomach content weights occurred in the evening (17:00–21:00 and 18:00–22:00), followed by significant increases (Mann-Whitney *U*-test, *P* < 0.05) at night (21:00–01:00 and 22:00–02:00), although at 21:00 and 22:00 sample sizes were small (*N* = 7; Fig. 5). A significant decrease (Mann-Whitney *U*-test, *P* < 0.05) was also observed in early morning (04:00–08:00), followed by a significant increase (Mann-Whitney *U*-test, *P* < 0.05) in the afternoon (12:00–16:00).

One-way ANCOVA's for each of the three sets of eight 3-h intervals revealed stomach content weights were not significantly different (*P* > 0.05) over time intervals (Fig. 5). In contrast, significant differences were found for two of the four sets of six 4-h intervals (Fig. 5). Overall, results from the Kruskal-Wallis and one-way ANCOVA's agreed in four of seven (57%) cases.

DISCUSSION

The percentage of empty stomachs found in this study (5%) is one of the lowest reported for shark species collected using nets or other non-bait methods of capture (Wetherbee et al., 1990) and agrees with Parsons (1987) who found 7% empty stomachs in *S. tiburo* from Tampa Bay. This suggests that *S. tiburo* eats frequently and/or that gastric evacuation is slow relative to feeding frequency.

Our results indicate that feeding in *S. tiburo* in Tampa Bay and Charlotte Harbor is very homogeneous. *S. tiburo* specializes on *C. sapidus*, while cephalopods and

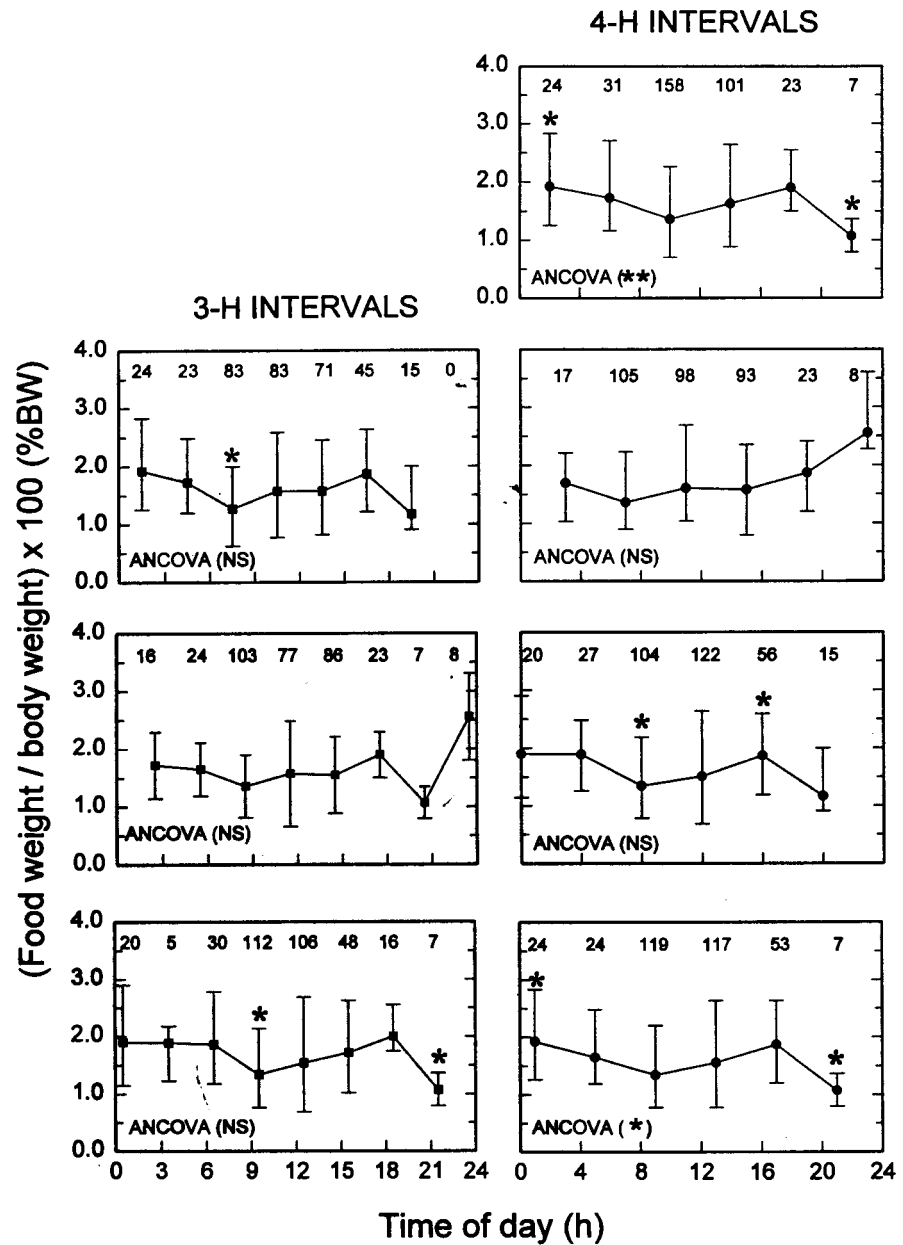


Figure 5. Diel variation in median amount of food in the stomachs of *Sphyrna tiburo* from southwest Florida, expressed as a percentage of wet body weight. Each value represents the mid-point of a given time interval. Solid squares (■) are the medians (with 25th and 75th percentiles) for three sets of eight 3-h intervals, starting at 00:00, 01:00, and 02:00, from top to bottom; solid circles (●) are the medians (with 25th and 75th percentiles) for four sets of six 4-h intervals, starting at 00:00, 01:00, 02:00, and 03:00, from top to bottom. Points with an asterisk above them were significantly different (Mann-Whitney *U*-test, $P < 0.05$) from those immediately preceding them. Results of one-way ANCOVA's are given in parentheses in the lower left corner of each graph: NS (non-significant) $P > 0.05$, * $P < 0.05$, ** $P < 0.01$. The number of stomachs examined for each time period is given at the top of each graph.

teleosts are relatively unimportant. Parsons (1987) also found high occurrences of *C. sapidus* in stomachs of *S. tiburo* from Tampa Bay, while cephalopods were the dominant prey item in Florida Bay. In our study, angiosperms were the second most important item and appeared in over 50% of the *S. tiburo* stomachs examined. Cortés and Gruber (1990) also reported that angiosperms were the second most important item in the stomachs of lemon sharks, *Negaprion brevirostris*, from the Florida Keys, occurring in a third of the stomachs examined. As suggested by them for the lemon shark, the presence of seagrasses in *S. tiburo* stomach contents probably reflects the benthic feeding habits of this species and may be completely incidental to prey capture, especially because their main prey, *C. sapidus*, feeds on seagrasses and associated epifauna (Zieman and Adams, 1982). Although the caloric content of seagrasses is high (4.470 kcal·g⁻¹ dry weight; Cummins and Wuycheck, 1971), elasmobranchs are not known to have an efficient mechanism for the maceration of plant material and appear to lack the digestive enzymes necessary to break it down (Fänge and Grove, 1979). Therefore, it is unlikely that *S. tiburo* derives any energy from ingesting seagrasses, except possibly by digesting epibionts present on the surface of the seagrasses. The possibility that ingested seagrasses may help protect the gastro-intestinal lining from injury by crustacean spines or other hard parts of prey items cannot be discounted and deserves further investigation.

While we found seasonal and habitat-related differences in the diet of *S. tiburo*, no significant dietary shifts associated with size of sharks were found. However, median stomach content weight to shark weight increased with increasing shark size. This was unexpected because daily ration of fishes generally decreases with increasing fish size (Pandian, 1967). In sharks, Van Dykhuizen and Mollet (1992) reported relative food intake levels 10 times higher for pups than for adults of the sevengill shark, *Notorynchus cepedianus*, held in captivity. The opposite trend in the weight of *S. tiburo* stomach contents could be due to a slowing down of digestion as individuals age (and grow)—a pattern well documented in teleosts (Fänge and Grove, 1979)—and to the increased difficulty of digesting larger prey items (Jobling, 1987). Since *S. tiburo* males mature at a shorter length than females (Parsons, 1993), this could also help explain why immature males had less food in their stomachs than immature females and all mature sharks. Studies of gastric evacuation and daily ration in *S. tiburo* are needed to help clarify this issue. Likewise, estimates of prey biomass and size composition are needed to determine whether the higher proportions of *C. sapidus* prey in the 14–24 mm range of carapace length (Fig. 4) are a result of size selectivity or just reflect prey availability in the study areas.

Rank correlation assessments of diet overlap are highly dependent on the number of food categories included in the analyses and the number of significant figures considered. When the number of categories is small, as was the case in our analyses, the estimate of agreement tends to be inflated and differences within lower-level categories are masked. In contrast, Horn's index of overlap (R_o) is not influenced by the number of food categories considered because it uses the relative proportions of each food type rather than assigning ranks. In all, diet overlap results indicate that the diet of *S. tiburo* is very uniform and only differs markedly between habitats. Evidence that most bonnethead sharks leave the bays in winter and some can be found off the beaches in winter (Hueter and Manire, 1994) implies that individual sharks undergo this diet shift when they switch between these habitats.

The values of diet breadth we found using three indices were generally low, attesting to the specialized nature of the feeding habits of *S. tiburo*. While the

Shannon-Wiener measure gives relatively more weight to the rare food categories, Levin's index gives more weight to the abundant food categories, and the combined index we used balances these two opposing trends.

Our conclusions on *S. tiburo* diel feeding chronology varied according to length of time intervals (3-h vs. 4-h), interval start, and statistics used. When 3-h time intervals were used and Kruskal-Wallis and Mann-Whitney *U*-tests were run, the results indicated that feeding was discontinuous (although not highly significant; $P < 0.05$) through the diel period in two of the three sets of eight 3-h time intervals chosen. With this approach, and assuming the stomach contents weight/body weight ratio reflects feeding activity, we would conclude that feeding in *S. tiburo* decreased in early morning, increased during the day hours, and decreased in the evening, depending on our choice of eight 3-h time intervals. In contrast, if we examine the results found by using 4-h intervals, our conclusion would be that feeding decreases in early morning, increases in the afternoon, decreases in the evening, and increases at night, depending on our choice of six 4-h time intervals. Furthermore, if ANCOVA's of stomach content weight vs. shark weight for each of the three sets of eight 3-h time intervals were used, our conclusion would be that feeding activity is not discontinuous with time. In contrast, if we ran ANCOVA's for each of the four sets of six 4-h time intervals, we would conclude that feeding is discontinuous with time in two of the four cases.

These results show that both the statistical treatment of the data and the length and choice of time intervals can influence the conclusions on diel feeding chronology in *S. tiburo*, and probably in other fishes as well. If results show absence of feeding discontinuity, it does not necessarily mean that feeding is continuous with time, because differences in feeding activity may not always be reflected by stomach content weight (Jenkins and Green, 1977). Diel feeding activity is a complex process resulting from interactions among various biotic and abiotic factors operating on behavioral and physiological processes related to feeding. To explain the large individual variations in feeding at any given time and the variations in feeding activity at different times found in many fish studies, we need a better understanding of these various factors and processes.

Despite these methodological shortcomings, we have shown that the diet of *S. tiburo* in Tampa Bay and Charlotte Harbor, Florida, is specialized, depends on season and habitat, and remains homogeneous between sexes, geographical locations, and shark sizes.

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